

## Growth Rates of Juvenile Pinfish (*Lagodon rhomboides*): Effects of Habitat and Predation Risk

STACEY L. HARTER\* and KENNETH L. HECK JR.

University of South Alabama, Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528

**ABSTRACT:** Predation is often the largest source of mortality for juvenile fish and the risk of predation can influence growth rates by either forcing young fish into suboptimal foraging habitats or reducing the amount of time spent foraging. We used field experiments to test effects of predation risk by gulf flounder (*Paralichthys albigutta*) on juvenile pinfish (*Lagodon rhomboides*) growth rates by measuring changes in length and weight in three habitats (sand, low density, and high density shoalgrass, *Halodule wrightii*) in Perdido Key, Florida. Benthic cores, seagrass samples, and stomach contents were also analyzed to examine differences in pinfish prey densities, grass densities and epiphyte coverage, and diet, respectively, among habitat and predator treatments. Both length and weight growth rates were determined and showed similar results. We found that pinfish inhabiting seagrass habitats, particularly low density *Halodule* displayed the fastest growth rates in the beginning of the growing season (June) and those in sand had the fastest growth rates later in the season (October). These differences in growth rates did not appear to be influenced by densities of pinfish prey items since the treatment having the highest density of prey was not that in which growth rates were the greatest. This seasonal shift may be attributed to increasing pinfish size. Larger pinfish in October may have been inhibited by high density grass, reducing foraging efficiency. These results demonstrate how occupying a suboptimal foraging habitat can affect juvenile pinfish growth rates. Predation risk significantly reduced length and weight growth rates of pinfish in June, but not October. This suggests that smaller pinfish early in the season traded time spent foraging for predator avoidance, while larger pinfish were likely to have reached a size refuge from predation. This study demonstrates that nonlethal effects from predation are also important influences on juvenile pinfish.

### Introduction

Predation plays a major role in determining the composition of juvenile fish assemblages by directly affecting size distribution (Wright et al. 1993) and survivorship (Carr and Hixon 1995), and indirectly influencing growth rates of newly-recruited juvenile fish (Diehl and Eklov 1995; Persson and Eklov 1995). Since vulnerability to predation is usually inversely related to size (Mittlebach and Chesson 1987; Levin et al. 1997; Sogard 1997), rapidly growing juvenile fish are more likely to survive to maturation, thereby influencing adult population size through size-selective mortality (Sogard 1997).

Optimal foraging theory predicts that consumers select prey types or habitats that maximize growth and fitness. When faced with a conflict between maximizing energy intake and avoiding predators, animals often do not respond as predicted by optimal foraging models (Milinski 1986). Prey species may use many different behaviors to avoid predation, one of the most common being selection of structurally complex habitats. Pinfish (*Lagodon*

*rhomboides*) used both seagrass and sand equally in the absence of predators, but increased use of seagrass when piscivorous southern flounder (*Paralichthys lethostigma*) were present (Jordan et al. 1996). An increase in structural complexity provides protection from predators (Werner and Hall 1988) due to a decrease in a predator's ability to detect and capture prey (Savino and Stein 1982). This holds true for the prey species as well, in that their own foraging efficiency is also reduced, so foraging success is traded off for effective predator avoidance.

Use of suboptimal foraging habitats by fishes can lead to reduced growth (Sogard 1994). Small bluegills (*Lepomis macrochirus*) hiding in a suboptimal foraging habitat (i.e., vegetation) grew up to 27% slower than small bluegills in open water (Werner et al. 1983). Reduced growth rates in suboptimal habitats are likely due to reduced foraging activity in the presence of a predator (Lima and Dill 1990) or reduced foraging efficiency in structured habitats.

To date, manipulative field studies combining effects of predation risk and habitat on growth rates of juvenile fish are rare in marine systems. The objectives of this study were two-fold: to evaluate effects of the presence of gulf flounder (*Paralichthys albigutta*), a piscivorous predator, on juvenile pinfish

\*Corresponding author; current address: National Oceanic and Atmospheric Administration Fisheries, Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, Florida 32408; tele: 850/234-6541 ext. 202; fax: 850/235-3559; e-mail: Stacey.Harter@noaa.gov

growth rates, and to examine growth rates of juvenile pinfish in different habitats of varying complexity. These objectives were accomplished by carrying out a field experiment that measured growth rates of pinfish in three densities of seagrass both with and without a flounder predator.

## Materials and Methods

### STUDY SITE

Experiments were conducted in monotypic stands of shoalgrass (*Halodule wrightii*) in Big Lagoon, Florida (30°18.5'N, 87°23.0'W), along the northern shore of the Gulf Islands National Seashore at Perdido Key. Environmental variables (i.e., temperature, salinity, and dissolved oxygen) were measured from the study site before and after each experiment using a YSI model 30 meter. Due to the close proximity of treatments (<15 m between treatments), physical factors including depth, wave action, turbidity, temperature, salinity, and dissolved oxygen did not differ significantly between them and behaved as expected throughout the course of the study. Temperatures ranged from 29.1°C to 31.1°C in June and 14.7°C to 24.4°C in October, salinity from 25.7‰ to 28.5‰ in June and 26.3‰ to 29.0‰ in October, and dissolved oxygen from 5.9 to 8.5 mg l<sup>-1</sup> in June and 8 mg l<sup>-1</sup> in October.

### EXPERIMENTAL ANIMALS

The prey for this study was juvenile pinfish, ranging in size from 50 to 100 mm total length (TL). Pinfish have a broad geographic range, inhabiting coastal waters from Massachusetts, United States, to Yucatan, Mexico (Hoese and Moore 1977). They spawn offshore and migrate into estuaries during spring and summer as juveniles (15–100 mm long; Wang and Kernehan 1979), where they remain until late fall, at which time they migrate back offshore to adult habitats. Juveniles are most abundant in structured habitat, such as seagrass, and rarely venture out onto open sand (Stoner 1979). Pinfish are the numerically dominant fish within seagrass habitat in shallow subtidal areas of the Gulf of Mexico (Stoner 1980) and are capable of having broad ecological effects on the flora and fauna of estuaries.

The predator used in this study was the gulf flounder, which is found on sandy substrates from Cape Lookout, North Carolina, to Corpus Christi, Texas (Böhlke and Chaplin 1993). We found that gulf flounder are also readily captured by trawling in seagrass beds. Adult gulf flounders are ambush predators and feed primarily on fish, including pinfish (Darnell 1958).

### Cage Construction and Experimental Design

Enclosures (1.41 × 1.41 × 1.25 m) with a volume of approximately 2 m<sup>3</sup> were used to restrict pinfish and flounder to specified habitats. Enclosures were constructed of polyethylene mesh with a mesh size of 0.64 cm tied to a welded reinforcement bar frame. They were anchored by sinking reinforcing bar legs of the cages into the sediment. To prevent burrowing animals from entering the enclosures, a 15-cm wide mesh skirt was placed around the bottom of each cage, which was anchored to the sediment with reinforcement bar hooks. Pilot studies indicated extra precautions were needed to prevent flounder from escaping by burrowing under the cage. Monofilament nylon gill netting with a mesh size of 5.72 cm was placed on the bottom of each cage, buried sufficiently deep in the sediment to allow for the normal burying behavior of the ambush style flounder predators. This size mesh was large enough to allow seagrass to come up through the net, but small enough to prevent flounder from gill netting themselves or escaping. Mesh tops were put on each cage so that fish, such as mullet (*Mugil cephalus*), could not jump inside.

Ten enclosures were deployed for each of the following habitat treatments: sand (i.e., no vegetation), low grass density, and high grass density for a total of 30 cages. Within each habitat treatment, 5 enclosures were controls stocked with pinfish only and 5 enclosures were experimental cages stocked with both pinfish and one flounder. Prior to stocking, cages were seined to remove fauna larger than the cage mesh size that could potentially prey upon juvenile pinfish or compete with them for food (for seining protocol, see Spitzer et al. 2000). The experiment was conducted two times: June and October 2001. During that time, cages were moved between the experiments due to seasonal thinning of grass inside some of the cages.

### Pinfish Growth Experiment - Changes in Length and Weight

Pinfish and predatory flounders were collected from grassbeds near the study area using a combination of otter trawls, gill netting, and dip nets. Prior to stocking, pinfish were measured (±1 mm TL), weighed (±0.1 g wet weight [ww]), and individually marked using a liquid nitrogen branding protocol (Spitzer et al. 2000). One flounder was placed in each experimental cage of each habitat treatment and was measured (±1 mm TL) prior to stocking. Flounder >250 mm TL were used in this study to ensure that gape size was large enough to actually pose a threat to pinfish. The smallest size fish that could not escape the enclosure mesh, which was about 40–45 mm TL, determined the size

of pinfish placed in enclosures for the initial experiment. The October experiment used the most abundant size found in trawls to mimic the natural increase in pinfish size as the growing season progresses.

Pinfish density stocked within the initial experimental enclosures was determined by density estimates of natural populations in the northern Gulf of Mexico reported by Thompson (2000). A trawling efficiency of 65% (Kjelson and Johnson 1978) was used to adjust densities of pinfish reported in Thompson (2000) to determine stocking density. The October experiment had a smaller fish density, mimicking the natural population decline that occurs as the growing season progresses.

Pinfish growth was measured by changes in length and weight. Each experiment lasted 3 wk, at which time pinfish were seined from each cage, measured ( $\pm 1$  mm TL), and weighed ( $\pm 0.1$  g ww). Flounder were also removed from the experimental cages and measured ( $\pm 1$  mm TL). Fish were kept on ice and brought back to the laboratory for stomach content analysis (see below).

Size ranges of pinfish and flounder stocked in cages, stocking densities of pinfish, and recapture rates of pinfish and flounder for each experiment are given in Table 1. To ensure that initial pinfish sizes did not significantly differ, one-way analysis of variance (ANOVA) or Kruskal-Wallis tests were run on lengths and weights of pinfish stocked in cages with either habitat or predator presence as factors. Lengths and weights of stocked pinfish did not significantly differ among habitats or predator treatments for any experiment ( $p > 0.050$ ).

Growth rates of individually marked pinfish were determined. Standardized differences ((Final – Initial)/Initial) in pinfish lengths and weights were calculated and divided by the number of days in each experiment to examine percent change in length or weight per day. Average percentages were obtained for each cage, which were then analyzed along a pinfish size gradient using two-way ANOVAs with habitat and predator presence as factors. Percent changes in pinfish length for the October experiment were square root transformed to correct for unequal variances. A three-way ANOVA with habitat, predator presence, and season could have been used, but this was not the best option since seasonal effects were anticipated. This would have resulted in significant interactions, precluding discussion of the main effects.

A number of predator treatment cages were without predators at the end of the experiment, which can be explained by either natural death or, more likely, escape. This was accounted for in the analyses so as not to bias the results. Length and weight growth rates were tested for significant

TABLE 1. Densities, size ranges, and recapture rates of marked pinfish and gulf flounder for each experiment (June 7–28 and October 15–November 1, 2001) in each habitat (sand, low density *Halodule*, and high density *Halodule*) and predator treatment (flounder absent and flounder present).<sup>a</sup>

	June	October
Range of pinfish length (mm TL)	45–65	73–107
Range of pinfish weight (g)	1.2–6.6	5.4–18.2
Pinfish m <sup>-2</sup>	8	5
# of pinfish tagged and caged	480	300
# of recaptured pinfish		
Sand	68	23
Low density grass	20	38
High density grass	61	22
Pinfish recapture rate (%)		
Sand	42.5	23.0
Low density grass	12.5	43.0
High density grass	38.1	23.0
Flounder absent	30.0	25.0
Flounder present	37.5	38.3
Overall pinfish recapture rate (%)	30.8	29.7
# of flounder stocked (1 cage <sup>-1</sup> )	15	15
Range of recovered flounder	310–380	250–410
Lengths (mm TL)		
# of recaptured flounder		
Sand	1	2
Low density grass	2	2
High density grass	1	2
Flounder recapture rate (%)		
Sand	20	40
Low density grass	40	40
High density grass	20	40
Overall flounder recapture rate	26.7	40

<sup>a</sup>Recapture rate for each treatment = # of fish recaptured in each treatment  $\times$  (# of fish tagged in each treatment)<sup>-1</sup>; Overall recapture rate = total # of marked fish recaptured for each experiment  $\times$  (total # of fish marked for each experiment)<sup>-1</sup>.

differences between no predator treatment cages and those that were missing flounder at the end of the experiment. No significant differences were observed ( $p > 0.050$ ), so data were combined and the only cages considered in the predator treatment were those that had a flounder present the entire experimental period.

For all analyses, a significance level of  $\alpha < 0.050$  was used. If interactions between treatments resulted from any two-way ANOVA, they were noted in the results. If pairwise comparisons were necessary, they were conducted with Fisher LSD tests. Transformations were used to correct for unequal variance or non-normality when necessary, but tables and graphs present nontransformed data so that comparisons could easily be made between treatments and experiments.

#### VEGETATION AND EPIPHYTE BIOMASS

Shoalgrass biomass was estimated using a two-inch diameter PVC corer (0.0016 m<sup>2</sup> area) in June.

Three cores were taken in each cage before and after the experiment. This method of sampling grass biomass was altered in October because leaf length became too great to fit into the corer. A 10 × 10 cm PVC quadrat was haphazardly thrown twice in each cage (except those in sand), and all aboveground biomass was harvested by hand from the quadrat. Seagrass was dried at 80°C for at least 24 h and weighed ( $\pm 0.0001$  g). Dried seagrass biomass (g dry weight [dw] m<sup>-2</sup>) was calculated. Initial and final samples were combined for each cage and cage averages were analyzed between habitats using paired *t*-tests for each experiment. This was done to ensure that two distinct densities of seagrass were maintained throughout the experiments.

Epiphyte biomass was also estimated from these grass samples. A subset of seagrass blades from each sample was randomly chosen and scraped free of epiphytes using a razor blade. The number of blades scraped depended on the amount of epiphytes on each blade. Just enough were scraped so that a difference in pan + sample weight could be observed from pan weight alone. Both epiphytes and scraped blades were dried for at least 24 h at 80°C and then weighed ( $\pm 0.0001$  g). Epiphyte biomass (g dw epiphytes (g dw scraped blade)<sup>-1</sup>) was calculated, and cage averages were analyzed using paired *t*-tests to test for habitat effects for each experiment.

#### BENTHIC FAUNA

Food densities could influence pinfish growth rates, so densities of potential pinfish prey were estimated before and after each experiment. Benthic fauna was sampled using a two-inch diameter PVC corer (area = 0.0016 m<sup>2</sup>) to a depth of 10 cm. Three samples were taken at random locations within each cage. In the lab, each core was washed over a 0.5-mm sieve and sorted for potential pinfish prey. All potential pinfish prey, including amphipods, isopods, caridean shrimp, and small crabs (Darnell 1958; Hansen 1969; Carr and Adams 1973), were counted and identified to the lowest possible taxon using a dissecting microscope. Initial and final samples were combined and cage averages of shrimp and amphipod densities, as well as total densities of all taxa combined, were tested with two-way ANOVAs to examine differences between enclosures with and without a predator and among habitats for each experiment. Total density data was square root transformed in June and log<sub>10</sub> transformed in October to correct for unequal variances. Amphipods are known to be a major constituent of juvenile pinfish diets (Carr and Adams 1973; Stoner 1979) and, based on stomach content results from this study, shrimp are also a key food source, which

is why these two groups were singled out and individually analyzed. Shrimp densities were log<sub>10</sub> transformed in June to correct for unequal variances; transformations failed to satisfy assumptions for amphipod densities in June. Effects of habitat and predation were analyzed separately for June amphipod densities using Kruskal-Wallis tests. Caution should be used when interpreting these data, because an interaction term could not be tested.

#### STOMACH CONTENT ANALYSIS OF PINFISH AND FLOUNDER

Stomach contents of three randomly chosen branded pinfish from each cage were examined to help explain treatment effects on growth rates and to document shifts in diet as pinfish size increased. Stomach contents of all recovered flounder were also analyzed. Items within each stomach were identified to the lowest possible taxon with a dissecting microscope (12× magnification), and each major taxon was dried at 80°C for at least 24 h and then weighed ( $\pm 0.0001$  g). Mean total weight of gut contents was calculated for each cage and tested with two-way ANOVAs for differences between enclosures with and without a predator and among habitats for each experiment. The percentage that each major taxon made up of the total gut content weight was calculated and any differences in these percentages among habitat treatments and predator treatments were qualitatively compared.

### Results

#### PINFISH GROWTH

Effects of habitat and predation risk on growth rates of pinfish in length for each experiment are presented in Fig. 1. Growth among habitats was significantly different in June ( $F_{2,22} = 4.083$ ,  $p = 0.036$ ), and pairwise comparisons showed that it was significantly higher in low density grass than sand ( $p = 0.011$ ). The presence of a predator also had a significant effect on length increases in June, with lower growth rates among pinfish threatened by predation ( $F_{1,22} = 10.538$ ,  $p = 0.005$ ). No significant differences were seen for pinfish length changes among habitats in October ( $F_{2,18} = 3.503$ ,  $p = 0.061$ ). Growth in length between predator treatments also did not significantly differ in October ( $F_{1,18} = 0.001$ ,  $p = 0.975$ ).

Changes in pinfish weight showed almost the same patterns as changes in length among habitats and between predator treatments for both experiments (Fig. 2). Differences of percent change in weight among habitats were significant in June ( $F_{2,22} = 6.557$ ,  $p = 0.008$ ), and pairwise comparisons showed that weight change was significantly higher in low density grass than sand ( $p = 0.002$ ).



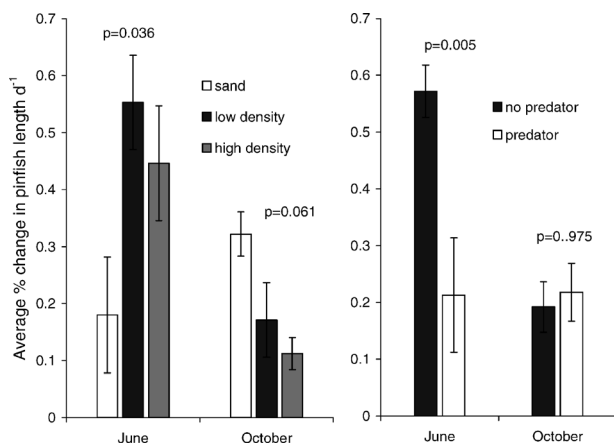


Fig. 1. Effect of habitat and predation risk on length growth rates of pinfish. Mean percent changes in length growth rates d<sup>-1</sup> (+SE) of pinfish recovered from the field enclosures among habitat and predator treatments for each experiment. p values represent results of two-way ANOVAs with habitat and predator as factors. Percent changes in pinfish length were square root transformed for October, but the untransformed data are presented for comparison purposes.

The presence of a predator significantly reduced weight growth rates of pinfish in June ( $F_{1,22} = 9.026$ ,  $p = 0.008$ ). In October, there was a significant difference in weight change among habitats ( $F_{2,18} = 10.936$ ,  $p = 0.002$ ), and pairwise comparisons demonstrated significantly more growth in sand than high density grass ( $p < 0.001$ ), as well as in low density grass than in high density grass ( $p = 0.006$ ). Changes in weight did not significantly differ between predator treatments in October ( $F_{1,18} = 3.055$ ,  $p = 0.104$ ).

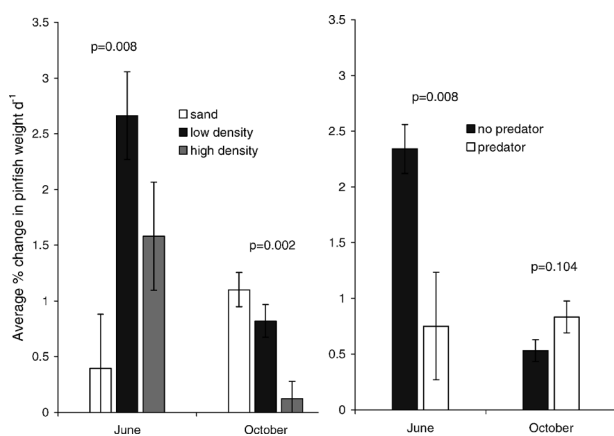


Fig. 2. Effect of habitat and predation risk on weight growth rates of pinfish. Mean percent changes in weight growth rates d<sup>-1</sup> (+SE) of pinfish recovered from the field enclosures among habitat and predator treatments for each experiment. p values represent results of two-way ANOVAs with habitat and predator as factors.

There were no significant interactions between habitat type and predator presence for length or weight in either of the experiments ( $p > 0.050$ ).

#### SEAGRASS AND EPIPHYTE BIOMASS

Dry weight of shoalgrass was significantly higher in high density grass than low density grass in both June ( $t = 2.09$ ,  $p = 0.029$ ,  $df = 19$ ) and October ( $t = 2.09$ ,  $p = 0.005$ ,  $df = 19$ ). During June, mean biomass was  $95.6 \pm 11.3$  g dw m<sup>-2</sup> for high density grass and  $64.1 \pm 10.2$  g dw m<sup>-2</sup> for low density grass. During October, mean biomass was  $100.7 \pm 15.9$  g dw m<sup>-2</sup> for high density grass and  $56.6 \pm 6.2$  g dw m<sup>-2</sup> for low density grass.

Epiphyte biomass in June was significantly higher in low density grass than high density grass ( $t = 2.09$ ,  $p < 0.001$ ,  $df = 19$ ); no significant difference was observed in October ( $t = 2.11$ ,  $p = 0.190$ ,  $df = 17$ ). Mean biomass during June was  $0.239 \pm 0.021$  g dw epiphyte (g dw scraped blade)<sup>-1</sup> for high density grass and  $0.458 \pm 0.037$  g dw epiphyte (g dw scraped blade)<sup>-1</sup> for low density grass. During October, mean biomass was  $0.146 \pm 0.014$  g dw epiphyte (g dw scraped blade)<sup>-1</sup> for high density grass and  $0.194 \pm 0.032$  g dw epiphyte (g dw scraped blade)<sup>-1</sup> for low density grass.

#### BENTHIC FAUNA

The most abundant faunal groups in the core samples were gastropods, amphipods, isopods, shrimp (penaeids, carideans, and alpheidids), mysids, crabs (xanthids and portunids), polychaetes, and bivalves. Small fish and chitons were rare and not considered in the analyses. Polychaetes were commonly found in the cores, but because most taxa are infaunal, they were not included in any analyses.

Total density of benthic fauna was significantly higher in seagrass habitats than in sand (Fig. 3) for both June ( $F_{2,59} = 10.16$ ,  $p < 0.001$ ) and October ( $F_{2,59} = 11.50$ ,  $p < 0.001$ ). In June, pairwise comparisons revealed a significantly greater density of fauna in high density grass than in sand ( $p = 0.001$ ). In October, pairwise comparisons showed a significantly higher density of fauna in both high density grass ( $p = 0.001$ ) and low density grass ( $p = 0.010$ ) compared to sand. Mean total number of organisms ranged from 1,292 to 7,177 m<sup>-2</sup> in sand, 4,698 to 27,542 m<sup>-2</sup> in low density grass, and 12,604 to 76,240 organisms m<sup>-2</sup> in high density grass. The drastic increase of faunal densities in high density grass samples in October was due to an explosion in the density of *Bittium varium*, the most abundant gastropod in the study area. Total density of benthic fauna did not significantly differ between cages with and without a predator ( $p > 0.050$ ).

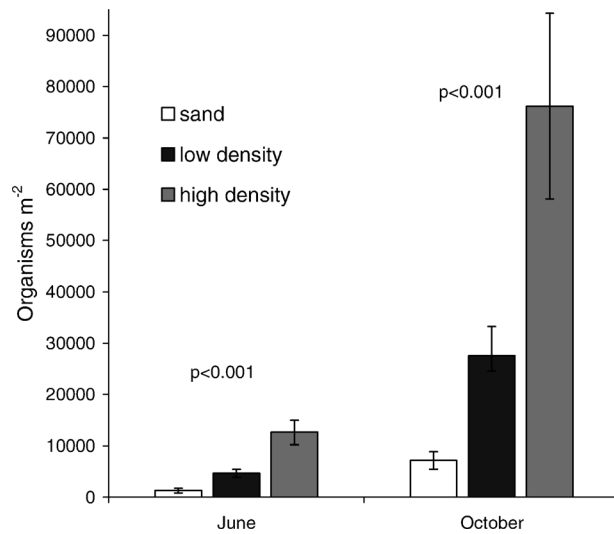


Fig. 3. Mean total number of benthic organisms  $m^{-2}$  (+SE) from core samples among habitat treatments for each experiment. p values represent results of two-way ANOVAs with habitat and predator as factors; predator presence was not a significant factor. Total density data was square root transformed in June and  $\log_{10}$  transformed in October, but the untransformed data are presented for comparison purposes.

Amphipod densities were significantly higher in high density grass during June ( $H = 15.69$ ,  $df = 2$ ,  $p < 0.001$ ) and October ( $F_{2,59} = 3.41$ ,  $p = 0.040$ ), but did not significantly differ between predator treatments ( $p > 0.050$ ; Fig. 4). Shrimp densities were not significantly different among habitats or between predator treatments for either experiment ( $p > 0.050$ ).

#### STOMACH CONTENTS

All flounder stomachs were empty at the time of collection except one, which contained two juvenile blue crabs (*Callinectes* sp.).

Only one of 160 pinfish stomachs analyzed was empty. Total weight of pinfish gut contents ranged from 0.2 g to 0.13 g and displayed a general seasonal increase (Fig. 5). Even though there were no significant differences in gut content weight among habitats ( $p > 0.050$ ), pinfish without the threat of predation had a higher mean gut content weight than those in the presence of a predator.

Shifts in taxa comprising the gut contents occurred as the season progressed (Fig. 6). In June, with the exception of unidentifiable digested animal material, the most commonly consumed taxa were shrimp, while plant material increased in abundance during October. Pinfish did not appear to consume different prey as a function of predator treatment in June; in October, pinfish with a predator consumed less plant material than those without a predator.

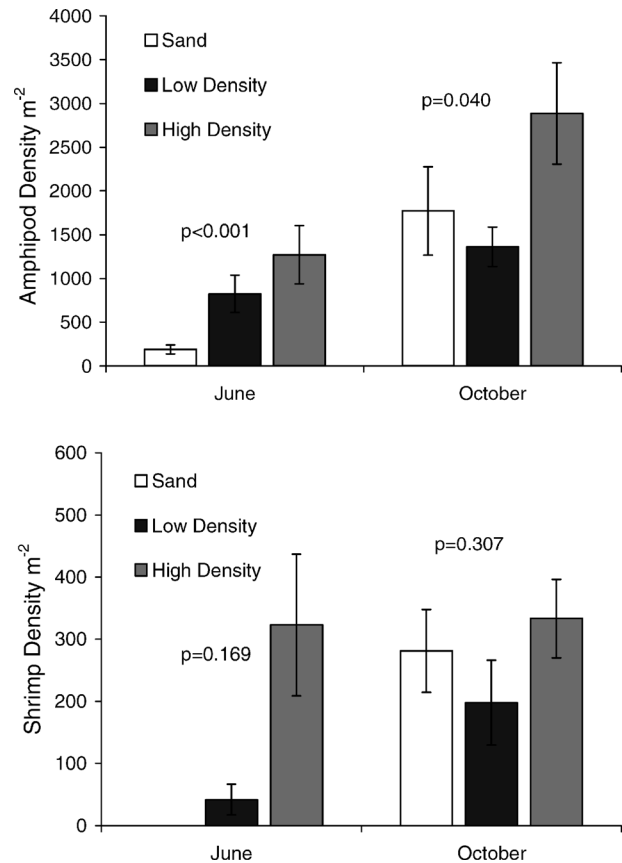


Fig. 4. Amphipod densities (top) and shrimp densities (bottom) (+SE) among habitat treatments for each experiment. p values for June and October shrimp densities and amphipod densities for October only represent results of two-way ANOVAs with habitat and predator as factors; predator presence was not a significant factor. Shrimp densities were  $\log_{10}$  in June, but the untransformed data are presented for comparison purposes. Transformations failed to satisfy assumptions for amphipod densities in June, so effects of habitat and predation were analyzed separately using Kruskal-Wallis tests; predator presence was not a significant factor.

#### Discussion

We found that risk of predation from gulf flounder significantly reduced growth rates of juvenile pinfish. Only a few other studies have examined predator-induced changes in growth rates of marine fish species, but all found that predation risk suppresses growth (Connell 1998; Steele 1998; Steele and Forrester 2002).

While the presence of a predator reduced growth rates of pinfish in June, this was not observed in October. This seasonal shift may be attributed to increasing pinfish size. Juvenile fish vulnerability to predation is inversely proportional to body size (Mittlebach and Chesson 1987; Sogard 1997), and pinfish in the latter part of the growing season may have reached a size refuge from predation. De-

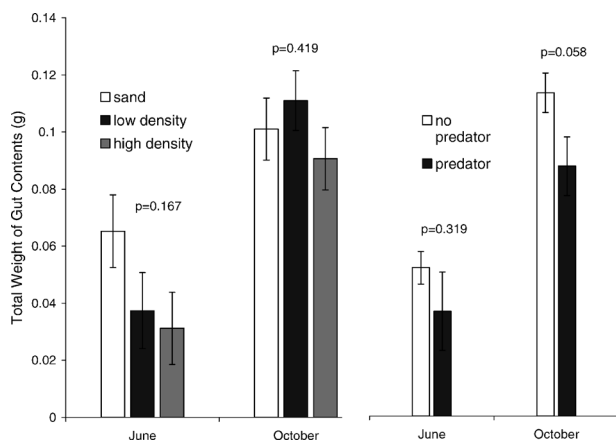


Fig. 5. Comparison of total weight of gut contents (g) (+SE) among habitat and predator treatments for each experiment. p values represent results of two-way ANOVAs with habitat and predator as factors; predator presence was not a significant factor.

creased vulnerability of larger juvenile fish may be explained by gape size limitation of the predator. Predators experience more difficulty capturing prey as they reach their gape size limit (Christensen 1996). Gape limitation can lead to size-dependent predation risk (Persson et al. 1996). Prior studies have found that flounder are capable of feeding on prey items 30–40% of their length (Hacunda 1981; Rice et al. 1993; Burke and Rice 2002). Rice et al. (1993) found that large southern flounder (160–200 mm TL) fed primarily on 60–70 mm TL spot (*Leiostomus xanthurus*), which is about 35% of their size in length. Applying this average to the pinfish

and flounder sizes used in this experiment, flounder posed a threat to pinfish in June; some of the larger pinfish in October probably exceeded the gape size of the predator, which could explain why no predator effects were observed for that experiment. This pattern of greater vulnerability of smaller fish to predation has been found in other studies. Growth rates were reduced by 27% for small bluegills (35 mm standard length) and enhanced by 11% for large bluegills (73 mm standard length) faced with the risk of predation by largemouth bass (*Micropterus salmoides*; Werner et al. 1983). Improved growth of large prey in the presence of predators, attributed to reduced competition for resources from smaller, more vulnerable conspecifics, was also seen with crucian carp (*Carassius carassius*) in the presence of predatory perch (*Perca fluviatilis*; Tonn et al. 1992).

Mechanisms by which predation reduces growth rates of juvenile fish include a reduction in foraging activity and movement to remain cryptic or a distributional shift in habitat, usually to a more complex one that may be a suboptimal foraging habitat. In a laboratory experiment, pinfish used both seagrass and sand equally in the absence of predators, but when a piscivorous southern flounder was introduced, pinfish avoided nonvegetated areas (Jordan et al. 1996).

In this study, we examined growth rates of pinfish in three different habitats and, again, a seasonal shift was noted. During the beginning of the growing season when pinfish were smallest, the fastest growth rates were observed in seagrass, especially low density of *H. wrightii*. This concurs with other studies examining the role of habitat complexity on growth of juvenile fish, which demonstrate that higher densities of seagrass inhibit fish from successfully capturing prey (Stoner 1982; Spitzer et al. 2000). Larger pinfish in the latter part of the growing season displayed faster growth rates in sand than either low or high density grass. Pinfish at this time of year may have reached a size where any density of vegetation hinders foraging efficiency and reduces swimming speed necessary to capture prey items (cf., Persson et al. 1998). Even larger juvenile pinfish are commonly found in seagrass habitats. This suggests that larger, more effective predators are present in nature to restrict larger juvenile pinfish to suboptimal foraging habitats.

Stomach contents failed to explain differences in growth rates among habitats and predator treatments, probably because such a large percentage was unidentifiable and only able to be separated into animal or plant categories. Had fish stomachs been injected with preservative immediately upon capture, this would have helped to provide more specific information. The high percentages of

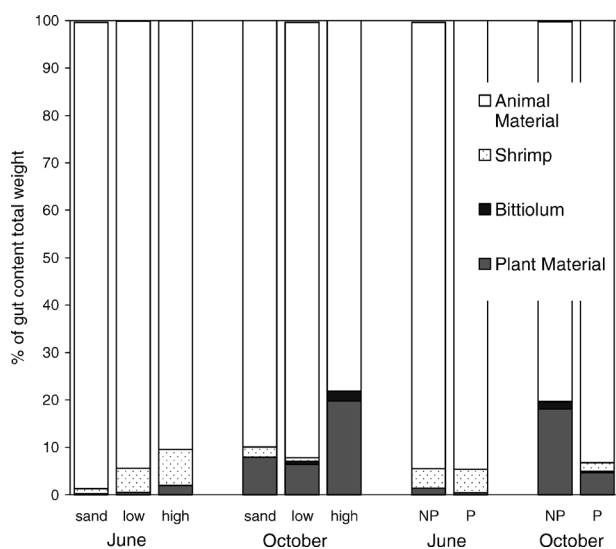


Fig. 6. Major taxa comprising the gut contents for each habitat and predator treatment for each experiment. Mean percent of gut content total weight for each major taxa group. NP = no predator, P = predator.

unidentified animal material are probably the result of continued digestion. Also, stomach contents of the fish are relevant only to the time period covered by the gut evacuation rate of the species. The data are only valid for the final hours of each experiment and not applicable to the overall experimental period. For these reasons, results from the gut content analysis need to be interpreted with caution. Of the taxa that could be identified, shrimp was the most consumed item in June in all habitats and predator treatments. In October pinfish consumed more plant material in all predator treatments and habitats. This demonstrates the increased tendency of larger pinfish towards herbivory (Stoner 1980; Weinstein et al. 1982). While plant material only accounted for as much as 20% of the gut contents in this study, other studies have found much higher percentages. Stoner (1980) found up to 91% of pinfish stomach contents were comprised of plant material. Percentages that high are not likely the result of incidental consumption, but rather an intentional targeting of detritus or live plant material. The observation that larger pinfish experienced highest growth rates in sand, yet consumed more plant material may seem contradictory, although, there are simple explanations for this; pinfish restricted to sand still have the opportunity to consume plant matter via detritus and drifting seagrass, and larger juvenile pinfish are not strictly herbivorous. Even though plant material increases in importance with pinfish size, those restricted to sand will also consume animal material, which may support a higher growth rate than plant material (Cui et al. 1992).

Prey densities for pinfish are obviously a major factor that could affect growth rates among habitats and predator treatments. As expected, core samples had consistently higher densities of benthic epifauna in seagrass habitats than in unvegetated habitats. The higher densities of prey items, together with the protection from predators that seagrasses provide, explain why a large number of recruiting fish are attracted to and use these habitats. This study suggests a greater role for seagrasses as predation refuge because the habitat that supported the highest density of potential prey was not the one in which pinfish grew fastest. Also, densities of benthic fauna were not significantly different between predator treatments. It appears that prey densities did not significantly influence growth rates in our experiments. Sand consistently supported the lowest density of fauna, yet growth rates of pinfish were greatest in sand during October, indicating that food was not limiting to pinfish in any habitat.

Field caging experiments, like the current one, that attempt to determine the combined effects of habitat and predation risk on the growth of

a particular species are rare in marine systems due to their difficulty. While more applicable to the real world than a laboratory experiment, we recognize that this study is still a simplification of nature. In nature, pinfish will encounter not only one, but many types of predators, and will also have numerous competitors for food and habitat. We also recognize the low return of both flounder and pinfish in this study; escape of target species being a familiar concern in caging experiments. The low return of flounder could not have affected the outcome of predator or habitat effects because it was taken into account in our analyses. Only those cages that had a flounder in them throughout the entire experimental period were considered predator treatment cages, and despite the low return of flounder and pinfish, significant differences were observed between predator treatments in June and among habitats for both experiments. Larger sample sizes only would have strengthened our argument.

In any caging study, one must consider potential artifacts. The one most relevant to this study is the possibility that cages may have acted as small fish and invertebrate attractors. A study conducted in the same area using the same cage structure, cage size, and mesh size found that cage structure had little effect on density and species composition of macrofauna inside the cage and that neither cage structure nor the inclusion or exclusion of pinfish had a notable effect on immigration and emigration rates of potential prey items (Gallagher 2001). Organisms should have immigrated and emigrated at similar rates into and out of the cage, keeping densities similar among cages and treatments.

Other studies examining growth rates of pinfish in seagrass found results comparable to ours. We found that growth in length averaged  $0.22 \text{ mm d}^{-1}$  in June and  $0.15 \text{ mm d}^{-1}$  in October in vegetated habitats, similar to Hansen (1969), who reported growth of juvenile pinfish in seagrass of the Pensacola estuary, Florida, to be  $0.32 \text{ mm d}^{-1}$  in spring,  $0.23 \text{ mm d}^{-1}$  in summer, and  $0.10 \text{ mm d}^{-1}$  in fall. Spitzer (2000) found somewhat higher growth rates for caged pinfish in seagrass in Perdido Bay, with rates ranging from  $0.43$  to  $0.66 \text{ mm d}^{-1}$  in summer and early fall but dropping off in late fall to around  $0.12 \text{ mm d}^{-1}$ . These higher values are most likely caused by the lack of predation effects due to the presence of cages.

The general consensus is that growth rates of estuarine-dependent fish are greater in vegetated compared to nonvegetated habitats (Heck et al. 2003). Growth rates of juvenile red drum (*Sciaenops ocellatus*) were twice as great in shoalgrass as nonvegetated bottom (Stunz et al. 2002). Pinfish in enclosures with both intertidal and subtidal



vegetation were approximately 90% heavier than fish in enclosures with intertidal vegetation and unvegetated subtidal bottom (Irlandi and Crawford 1997). Surprisingly, other studies have obtained conflicting results. Growth rates for juvenile red drum were higher in sand compared to shoalgrass (Nadeau 1991), but no difference in growth rates between vegetated and nonvegetated substrates were found for juvenile spotted sea trout (*Cynoscion nebulosus*; Heck and Nadeau unpublished manuscript). Specific species or location differences in growth rates may explain these variable results. The species of seagrass may alter outcomes as well. Stoner (1982) discovered that of three species of seagrass, shoalgrass provided the least protection for pinfish prey.

#### *Implications for Differences in Growth Rates*

Small differences in growth rates can produce significant changes in adult population size by either directly controlling the number of individuals reaching maturity (Jones 1991) or indirectly through size-selective mortality on juveniles (Sogard 1997). When predation slows growth, maturation is delayed and fewer individuals survive to maturity (Jones 1991). Because rapidly growing fish spend less time vulnerable to predation and are more likely to survive, recruitment levels are increased (Tonn et al. 1992). Faster growing fish also gain a survival advantage over slower growing fish via enhanced resistance to starvation and better tolerance of environmental extremes (Sogard 1997).

While many studies have focused on the lethal effects of predation on juvenile fish, this study demonstrates that nonlethal effects are also important influences on juveniles. By apparently reducing the amount of time spent foraging, predatory gulf flounder had a negative effect on growth rates of juvenile pinfish. In the natural environment (without cages present), the common response of juvenile fish to redistribute themselves among habitats in the presence of a predator can also affect recruitment to the adult stock by reducing growth rates in suboptimal foraging habitats.

#### *Acknowledgments*

We would like to thank John Valentine and Susan Sogard for guidance and support during this project, the numerous graduate students, technicians, lab assistants, interns, and REU's (Research Experience for Undergraduates program recipients) who helped with fieldwork, and the Dauphin Island Sea Lab Maintenance staff for preparing materials for field studies. The Gulf Specimen Marine Lab in Panama, Florida, provided assistance with flounder collection. Dauphin Island Sea Lab, University of South Alabama, Alabama Center for Estuarine Studies (ACES), Barber Fellowship, and Mississippi-Alabama Sea Grant Consortium all provided financial support for this project. This is Dauphin Island Contribution #375.

#### *LITERATURE CITED*

- BÖHLKE, J. E. AND C. C. G. CHAPLIN. 1993. Fishes of the Bahamas and Adjacent Tropical Waters, 2nd edition. University of Texas Press, Austin, Texas.
- BURKE, B. J. AND J. A. RICE. 2002. A linked foraging and bioenergetics model for southern flounder. *Transactions of the American Fisheries Society* 131:120–131.
- CARR, W. E. S. AND C. A. ADAMS. 1973. Food habits of juvenile marine fishes occupying seagrass in estuarine zones near Crystal River, Florida. *Transactions of the American Fisheries Society* 102: 511–540.
- CARR, M. H. AND M. A. HIXON. 1995. Predation effects on early post-settlement survivorship of coral reef fishes. *Marine Ecology Progress Series* 124:31–42.
- CHRISTENSEN, B. 1996. Predator foraging capabilities and prey antipredator behaviors: Pre- versus postcapture constraints on size-dependent predator-prey interaction. *Oikos* 76:368–380.
- CONNELL, S. D. 1998. Effects of predators on growth, mortality, and abundance of a juvenile reef-fish: Evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* 169:251–261.
- CUI, Y., X. LUI, S. WANG, AND S. CHEN. 1992. Growth and energy budget in young grass carp, *Ctenopharyngodon idella*, fed plant and animal diets. *Journal of Fish Biology* 41:231–238.
- DARNELL, R. M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Publications of the Institute of Marine Science University of Texas* 5:353–416.
- DIEHL, S. AND P. EKLOV. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. *Ecology* 76:1712–1726.
- GALLAGHER, L. 2001. An evaluation of potential artifacts associated with conducting caging experiments in a seagrass environment. M.S. Thesis, University of South Alabama, Mobile, Alabama.
- HACUNDA, J. S. 1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. *Fishery Bulletin* 79:775–788.
- HANSEN, D. J. 1969. Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulates*, near Pensacola, Florida, 1963–65. *Fishery Bulletin* 68:135–146.
- HECK, JR., K. L., G. HAYS, AND R. J. ORTH. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123–136.
- HOESE, H. D. AND R. H. MOORE. 1977. Fishes of the Gulf of Mexico: Texas, Louisiana, and Adjacent Waters. Texas A&M University Press, College Station, Texas.
- IRLANDI, E. A. AND M. K. CRAWFORD. 1997. Habitat linkages: The effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110:222–230.
- JONES, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: A multifactorial perspective, p. 294–328. In P. F. Sale (ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, California.
- JORDAN, F., M. BAROLINI, C. NELSON, P. E. PATTERSON, AND H. L. SOULEN. 1996. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides*. *Journal of Experimental Marine Biology and Ecology* 208:45–56.
- KJELSON, M. A. AND G. N. JOHNSON. 1978. Catch efficiencies of a 6.1 meter otter trawl for estuarine fish populations. *Transactions of the American Fisheries Society* 107:246–254.
- LEVIN, P., R. PETRIK, AND J. MALONE. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* 112:55–63.
- LIMA, S. L. AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.

- MILINSKI, M. 1986. Constraints placed by predators on feeding behaviour, p. 236–252. In T. J. Pitcher (ed.), *The Behaviour of Teleost Fishes*. Croom Helm, London, U.K.
- MITTLEBACH, G. G. AND P. L. CHESSON. 1987. Predation risk: Indirect effects on fish populations, p. 315–332. In W. C. Kerfoot and A. Sih (eds.), *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover and London.
- NADEAU, D. A. 1991. Relative growth rates of predatory fishes in vegetated and unvegetated habitats: Field experiments with juvenile red drum, *Sciaenops ocellatus*. M.S. Thesis, University of South Alabama, Mobile, Alabama.
- PERSSON, L., J. ANDERSSON, E. WAHLSTROM, AND P. EKLOV. 1996. Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. *Ecology* 77:900–911.
- PERSSON, L. AND P. EKLOV. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76:70–81.
- PERSSON, L., K. LEONARDSSON, A. M. DE ROOS, M. GYLLENBERG, AND B. CHRISTENSEN. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* 54:270–293.
- RICE, J. A., L. B. CROWDER, AND K. A. ROSE. 1993. Interactions between size-structured predator and prey populations: Experimental test and model comparison. *Transactions of the American Fisheries Society* 122:481–491.
- SAVINO, J. F. AND R. A. STEIN. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* 111:255–266.
- SOGARD, S. M. 1994. Use of suboptimal foraging habitats by fishes: Consequences to growth and survival, p. 103–132. In D. J. Stouder, K. L. Fresh, and R. J. Feller (eds.), *Theory and Application of Fish Feeding Ecology*. University of South Carolina Press, Columbia, South Carolina.
- SOGARD, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science* 60:1129–1157.
- SPITZER, P. M., J. MATTILA, AND K. L. HECK JR. 2000. The effects of vegetation density on the relative growth rates of juvenile pinfish, *Lagodon rhomboides*, in Big Lagoon, Florida. *Journal of Experimental Marine Biology and Ecology* 244:67–86.
- STEELE, M. A. 1998. The relative importance of predation and competition in two reef fishes. *Oecologia* 115:222–232.
- STEELE, M. A. AND G. E. FORRESTER. 2002. Variation in the relative importance of sublethal effects of predators and competitors on growth of a temperate reef fish. *Marine Ecology Progress Series* 237:233–245.
- STONER, A. W. 1979. Species-specific predation on amphipod crustacea by the pinfish *Lagodon rhomboides* mediated by macrophyte standing crop. *Marine Biology* 55:201–207.
- STONER, A. W. 1980. The feeding ecology of *Lagodon rhomboides*: Variation and functional responses. *Fishery Bulletin* 78:337–352.
- STONER, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides*. *Journal of Experimental Marine Biology and Ecology* 58:271–284.
- STUNTZ, G. W., T. J. MINELLO, AND P. S. LEVIN. 2002. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. *Marine Ecology Progress Series* 238:227–236.
- THOMPSON, K. 2000. Feeding ecology and production of the pinfish *Lagodon rhomboides* in temperate seagrass meadows. Ph.D. Dissertation, University of South Alabama, Mobile, Alabama.
- TONN, W. M., C. A. PASKOWSKI, AND I. J. HOLOPAINEN. 1992. Piscivory and recruitment: Mechanisms structuring prey populations in small lakes. *Ecology* 73:951–958.
- WANG, J. C. S. AND R. J. KERNEHAN. 1979. Sparidae porgies, p. 227–229. In R. D. Hoyt (ed.), *Fishes of the Delaware Estuaries: A Guide to the Early Life Histories*. Ecological Analysts Inc, Towson, Maryland.
- WEINSTEIN, M. P., K. L. HECK, JR., P. E. GIEBEL, AND J. E. GATES. 1982. The role of herbivory in pinfish (*Lagodon rhomboides*): A preliminary investigation. *Bulletin of Marine Science* 32:791–795.
- WERNER, E. E. AND D. J. HALL. 1988. Ontogenetic habitat shifts in bluegill: The foraging rate- predation risk trade-off. *Ecology* 69:1352–1366.
- WERNER, E. E., G. G. MITTLEBACH, D. J. HALL, AND J. F. GILLIAM. 1983. Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. *Ecology* 64:1525–1539.
- WRIGHT, R. A., L. B. CROWDER, AND T. H. MARTIN. 1993. The effects of predation on the survival and size-distribution of estuarine fishes: An experimental approach. *Environmental Biology of Fishes* 36:291–300.

#### SOURCE OF UNPUBLISHED MATERIALS

HECK, JR., K. L. AND D. A. NADEAU. unpublished manuscript. Marine Biology Department, University of South Alabama, 101 Bienville Boulevard, Dauphin Island, Alabama 36528.

Received, April 18, 2005

Revised, November 16, 2005

Accepted, December 7, 2005